Vision, pigments and structural colouration of butterflies

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Chapter 8

In the Realm of the Senses

Essay

The classification of five external senses of humans, attributed to Aristotle, is: vision, hearing, smell, taste, touch. Vision and hearing convey *spatial information* from the remote environment and are therefore *the remote imaging senses*. Aquatic vertebrates are using two more senses to image the environment: electroreception and the lateral line, implementing *remote touch*. The human sense of touch may be regarded as an aberrant imaging sense since it does not operate remotely and since it is most often used in the scanning mode (e.g. reading Braille). Chemical senses do not have continuous modalities (e.g. frequency, colour) but stimulus classes (e.g. sweet, sour). Chemical senses are also without the spatial modality; in order to get the spatial picture, an animal needs to scan the environment, e.g. by sniffing. Many animals rely heavily on smelling pheromone plumes to track their conspecifics and their physiological state. There is evidence that the humans are also not stripped of this sense, nor able to ignore it completely. In the case of humans, and many other animals living in illuminated environments, vision is the important sense. What makes vision special?

Vision extracts the information from light, a medium that conveys signals over distances, for all practical earthly living purposes instantly, preserving the directionality of the signal; in other words, light is a medium conveying information about the environment. Moreover, light, due to its wave nature, has two submodalities - wavelength and polarisation – which both can convey information. Vision can remain a passive sense in all environments where there is ambient illumination: practically all materials reflect at least a few percent of the incident light, and the energy that fuels transfer of information is ultimately provided by the Sun (or the stars). The detection is fully passive and static in the sense that it works without either the receiver or sender of the information actively emitting light. The workable range of vision as a passive sense spans from broad sunlight to a starry night, or in water, down to depths of several hundred metres. Further towards the bottom, vision cannot remain passive. Deep water fish often have special light organs.

In some other murky aquatic environments, such as turbid terrestrial waters and caves, active light organs would be either bringing more harm than good, or would simply be too energetically demanding. In these environments, vision is often excelled or completely replaced by one of the two other senses that retain directionality: electroreception and remote touch, as implemented by the fish lateral line (also known as svenning, after its discoverer Sven Dijkgraaf). These two senses have a limited range, due to the fact that they are near field detectors. Their range is directly proportional to the physical size of the sensor array. Further, their acuity is directly proportional to the spacing between the elements of the array, due to the fact that they are not using focussing optics. These two senses are hardly simultaneously static and passive, because the flow of energy is less constant and predictable in the case of mechanical waves and electrical waves than in the case of light. As a consequence, either stationary objects cannot be readily detected or the receiver must reveal itself by emitting energy that would then be reflected from stationary objects (e.g. production of the electric field in weakly electric fish, or any kind of self-movement for svenning).

While terrestrial arthropods do use mechanoreceptors to detect air flow, a full analogue of the lateral line has not yet been found. The physical constraints of a low-density medium and a relatively small body size prohibit this sense from having imaging capacity that would extend significantly into the environment. Terrestrial vertebrates have lost the ability of either remote touch and electroreception. In most terrestrial animals groups, hearing became an important accessory, or sometimes the main sense. Hearing (i.e. detection of far-field mechanical waves) is a sense developed in both terrestrial and aquatic forms of most animal groups. Binaural hearing however cannot provide a full image of the environment, because it relies on comparison between only two sensory units; for a more precise determination of the sensory image, binaural hearing is often used in conjunction with scanning (e.g. turning the ears or the body). Sometimes, especially in dark environments, binaural scanning combined with emission of energy, prevails over vision. The terrestrial case for this is the sonar of bats; the wet case are dolphins and whales.

Going beyond the intuitive understanding of information extraction, the concept of *information capacity* of any sense, but especially of vision, may be quantified with a rather computerised unit of bits per second. The information capacity is related to *the signal to noise ratio* and vision is often optimised for that. The flow of visual information can be overwhelmingly large; however, not all information may be relevant: the signals from static background structures may not always be informative. We can therefore use the concept of *relevant information capacity* and *the signal-to-background ratio*. Vision is optimised to extract the relevant signals from the environment and filter out the irrelevant ones. The neural mechanisms downstream further reduce the information and abstract the relevant signal to the point where the nervous system will make a behavioural decision that will be executed by the motor circuitry: attack or retreat, turn left or right. An important concept here is also, that extraction if information costs energy: more bits need more ATP.

The information yielded from the environment is often enhanced by combining the input from several senses or several modalities of the same sense. We may combine sound frequency and direction while we are subconsciously separating *the basso continuo* from the flamboyant voix singing *Cadró, ma qual si mira*. We may combine smell and vision to locate the defunct power transistor on the electronic board. We may make combined use of smell, vision and hearing in order to make an educated (?) guess about the genetic compatibility with the person who just entered the party. Humans and birds wear shiny feathers to be statically noticed. When they sing and dance, the display becomes even more persuasive. In the case of butterflies, the pheromones may be used to attract the conspecifics from a distance. From close, the adornment on the wings seems to be the medium they use to present their genetic quality. The display, be it static (e.g. the pattern of spots) or dynamic (e.g. wing flapping), must be tuned to the vision of the species. As these traits are under sexual selection, we may expect that the tuning will be mercilessly efficient. To complicate things further, a butterfly does not live in a benevolent environment: predators, too, can also use the colouration to detect the butterfly. The colouration is tuned both to the environment and to its vision, often walking on the thin line between being conspicuous and concealed. A similar triangle exist also between hearing, sound production and environment. However, when comparing colouration with sound production, the principle of passivity is again there: colourful adornment is static and will be seen when the two interacting conspecifics are in line of sight, while sound production requires energy and will potentially be detectable in a larger space.

Several aspects of a particular sense must be considered in the studies: the physical modalities, temporal precision, spatial acuity, reach (contact, near field, far field), imaging and scanning capability, the source of energy (the sensor itself, the detected object, extrinsic source), the relevant information, the background, the intrinsic noise. When adding to the picture the animal's interest in its conspecifics, the aspects of visibility and conspicuousness come into play. The lack of our own experience of a modality sometimes shows up in the lack of research and even the lack of the word for the sense. Outside mammals, UV and polarisation vision reveals a world which looks different than ours. The lateral line sense of amphibians and fish has been named with a synthetic expression (remote touch) and, less well known, with a novel word *svenning*. Although the major interest in studying this sense is due to the fact that it shares the sensory cell type (hair cells) with human hearing, a paradigm-shifting research of the field is more likely to be about how the image of the world is *svenned* by the lateral line.

Even more radically, although vertebrates sense pheromones with a special organ (the vomero-nasal organ of Jacobsen) with has a special neural connection with the brain (terminal cranial nerve, nerve zero), there is no word that would describe the sense, though the sensing action itself is named from German as *flehmen response* (the lip-rolling behaviour seen in horses; an overdone human pendant was simulated by Anthony Hopkins in the film *Silence of the Lambs*). The English verb could be *to flehm (-ed, -ing)*, the adjective *flehmy* or *flehmish*. An alternative English word to describe the sense could be a chimera made from pheromone smell; thus, *phell* as the noun, *to phell* (-ed, -ed, -ing) as the verb, and *phelly* as the adjective. The naming for the sense seems to be due also because it seems more and more plausible that humans, too, sense pheromones.

A student of sensory neuroscience should not be ignorant due to its own disability to detect a certain modality and should care not to get biased by the limitations of its own senses, when the modality is detected by the humans. This way, sensory neuroscience will be able to advance in the directions where biodiversity will provide for new concepts and maybe an extension of the list of external senses. These new paradigms may eventually be put into human use via biomimetics.